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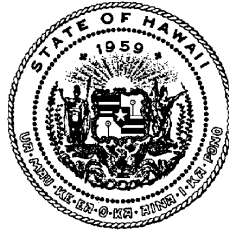
**Division of
Aquatic Resources**

Technical Report
20-01



A review of the biology of the family Carangidae, with emphasis on species found in Hawaiian waters

October 2000



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DIVISION OF AQUATIC RESOURCES

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Cover: *Caranx sexfasciatus*
photo by Michael R. Porter

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Introduction

The family Carangidae encompasses a diverse group of fishes known variously by such common names as jacks, trevallies (crevalles), amberjacks, pompanos, scads, kingfish, pilotfish, rainbow runners, among others. A considerable amount of the available literature deals with species of greatest economic importance, especially pompanos of the genus *Trachinotus*, which do not occur in Hawai‘i. The focus of this paper is on species found in Hawaiian waters, although many of the studies referenced were conducted in other parts of the world.

Taxonomic History

The family is named for the genus *Caranx*, first described by Lacépède in 1801. Previous descriptions of some carangid species, but assigned to other genera, include those by Artedi (1738), Osbeck (1757), Linnaeus (1758), Forsskål (1775), and Bloch (1793). Linnaeus originally placed members of the carangid genera *Naucrates* and *Trachinotus* in the genus *Gasterosteus* (the sticklebacks), and in 1766 described the related cobia (*Rachycentron canadum*) as *Gasterosteus canadus*. Forsskål and Bloch assigned various carangids to the genus *Scomber* (the mackerels). Quoy and Gaimard (1824) described carangids captured during their voyage around the world, and Cuvier and Valenciennes (1833) did early work on Indo-Pacific species. Descriptions of carangids in Hawaiian waters were included in works by Jordan and Everman (1903) and Fowler (1928).

A considerable amount of revision in nomenclature has occurred over the years. For example, Smith-Vaniz and Randall (1994) note that 16 junior names have been proposed for the white trevally (*Pseudocaranx dentex*). Bleeker (1852) and Berg (1947) list several carangid genera as belonging to the family Seriolidae, but that name is obsolete.

Carangids belong to the order Perciformes, suborder Percoidei, and superfamily Percoidea. The family is divided into four subfamilies (tribes), originally described by Starks (1911): Trachinotini, Scomberoidini, Naucratiini, and Carangini. Eschmeyer (1990) lists 122 generic names that have been ascribed to carangids at one time or another. There are now considered to be about 32 genera and 140 species worldwide (Nelson 1994). 24 species from 13 genera occur in Hawai‘i (Randall 1996, Suzumoto pers. comm.). In addition, the green jack, *Caranx cabalus*, may be establishing itself in Hawaiian waters (Randall 1999), but is not included here.

Phylogenetic relationships within the suborder and family remain poorly defined (Laroche et al. 1984). Freihof (1978) noted that the families Nematistiidae (roosterfish), Echeneidae (remoras), Rachycentridae (cobia), Coryphaenidae (dolphinfish or mahimahi), and Carangidae possess an apparent specialization of the lateralis system in the form of one or two tubular ossifications around the anterior extension of the nasal canal. This characteristic is rare in percoids, and suggests these families form a monophyletic group, the carangoids (Figure 1).

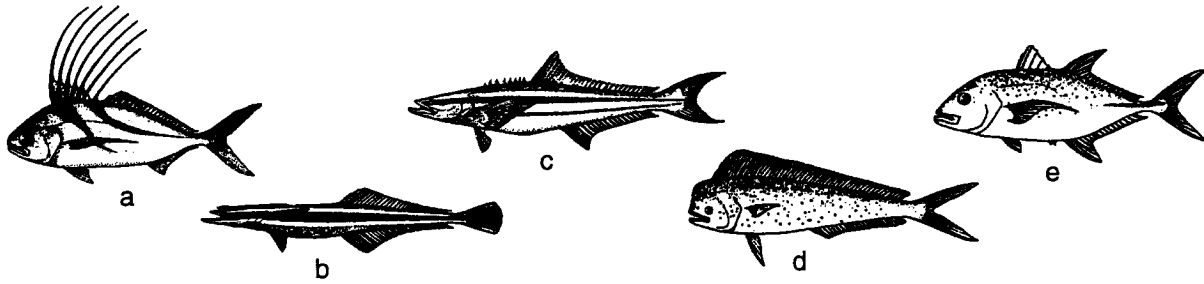


Figure 1

Representatives of the five families of carangoid fishes. (a) Roosterfish - Nematistiidae, (b) remora - Echeneidae, (c) cobia - Rachycentridae, (d) dolphinfin - Coryphaenidae, (e) trevally - Carangidae. (a) After Eschmeyer and Herald (1983), (b) and (c) after McClane (1974), (d) and (e) from Squire and Smith (1977)

Johnson (1984) further notes that these five families share small, adherent cycloid scales, and lists three synapomorphies that suggest Carangidae, Coryphaenidae, Rachycentridae, and Echeneidae are united as a monophyletic group: lack of the bony stay posterior to the ultimate dorsal and anal pterygiophores found in nearly all other percoids, presence of two prenasal canal units, and a lamellar expansion along the anterior margin of the coracoid. Hypothesized relationships among these groups are shown in Figure 2, based on characteristics described by Smith-Vaniz (1984a).

The roosterfish *Nematistius* has sometimes been regarded as a member of Carangidae, but is now considered a sister group of the other four families listed above. Nelson (1984) placed the species *Parastromateus niger* in its own family, Apolectidae (Formionidae), but in 1994 followed Smith-Vaniz (1984a) and placed it in Carangidae.

Gushiken (1988) described a hypothetical phylogenetic tree for the carangids (Figure 3). Presumed relationships were based on 25 characteristics that include gap between last two anal spines, upper jaw, detached or semidetached finlets, scutes, adipose eyelids, pharyngeal and premaxillary teeth, and a number of other muscular and skeletal features. As an example of the taxonomic confusion in the family, Gushiken considered *Kaiwarinus* a sister genus to *Pseudocaranx*, whereas Eschmeyer (1990) lists *Kaiwarinus* as a synonym of *Carangoides*. Smith-Vaniz is currently revising the genera *Pseudocaranx*, *Caranx*, and *Decapterus*, which will eventually result in further changes in nomenclature.

Diagnosis

Members of the family Carangidae are characterized by an anal fin with two anterior spines (one spine in *Elagatis* and *Seriolina*) separated from the rest of the fin, but which often become embedded with age (Figure 4). The caudal peduncle is very slender, and the caudal fin is deeply forked. The dorsal fin is generally divided into an anterior portion with four to eight

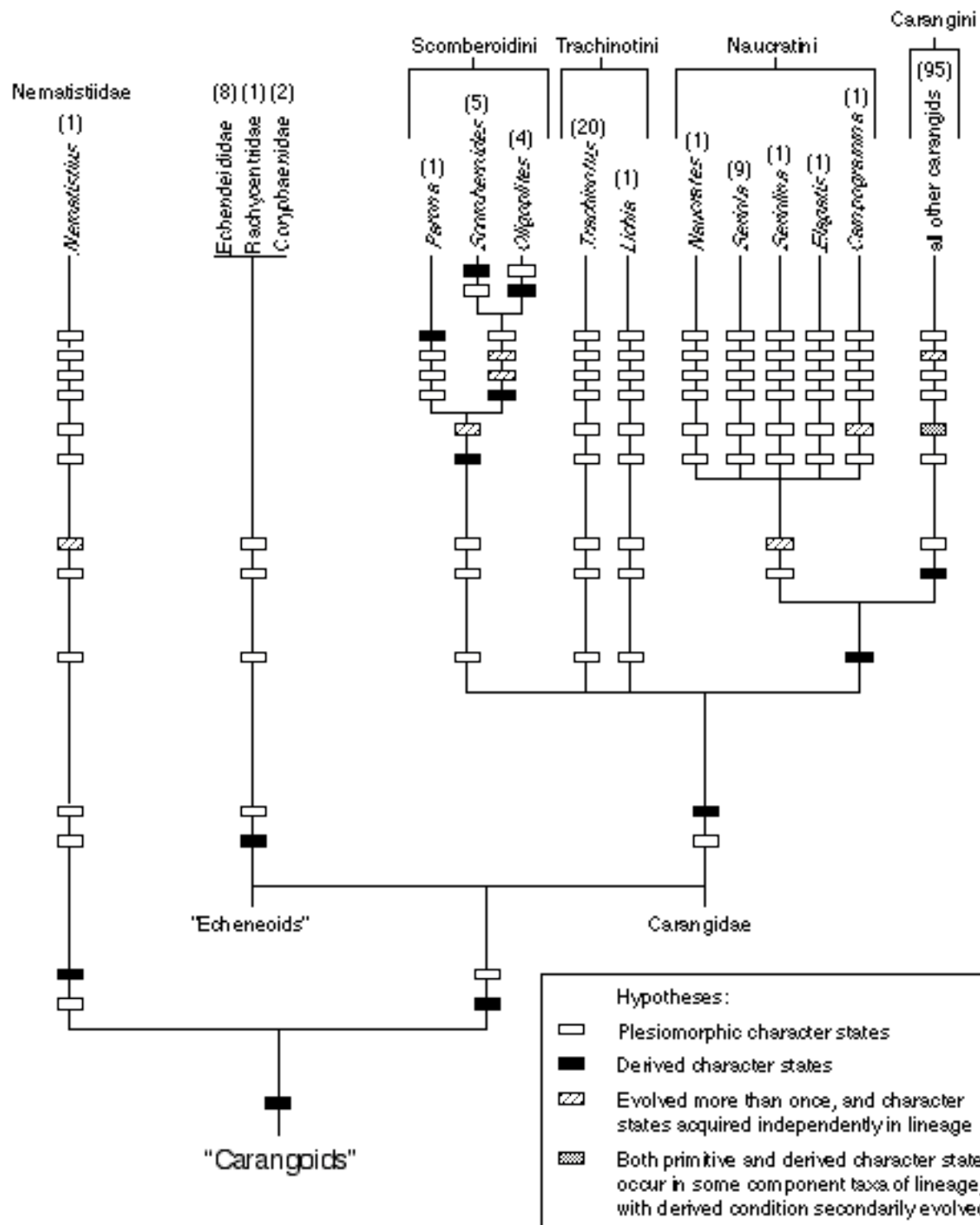


Figure 2

Hypothesized cladogram of carangoid fishes including main groups of Carangidae. Numbers in parentheses are estimated total number of species in taxon. After Smith-Vaniz (1984a).

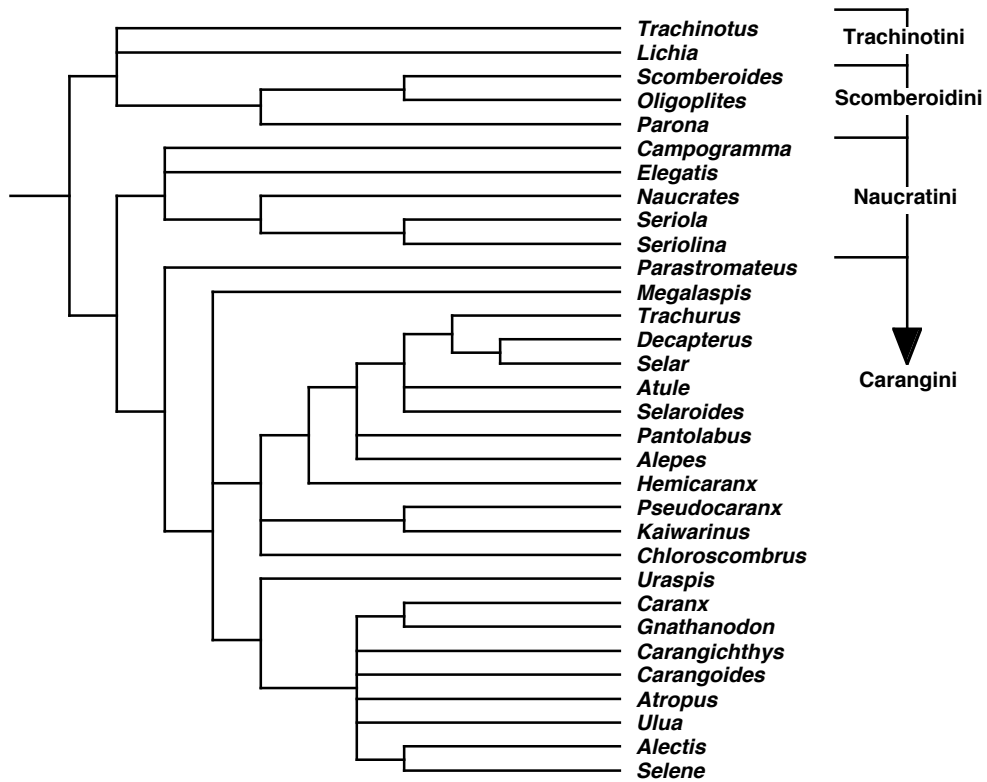


Figure 3

Hypothetical phylogenetic tree of the family Carangidae. After Gushiken (1988).

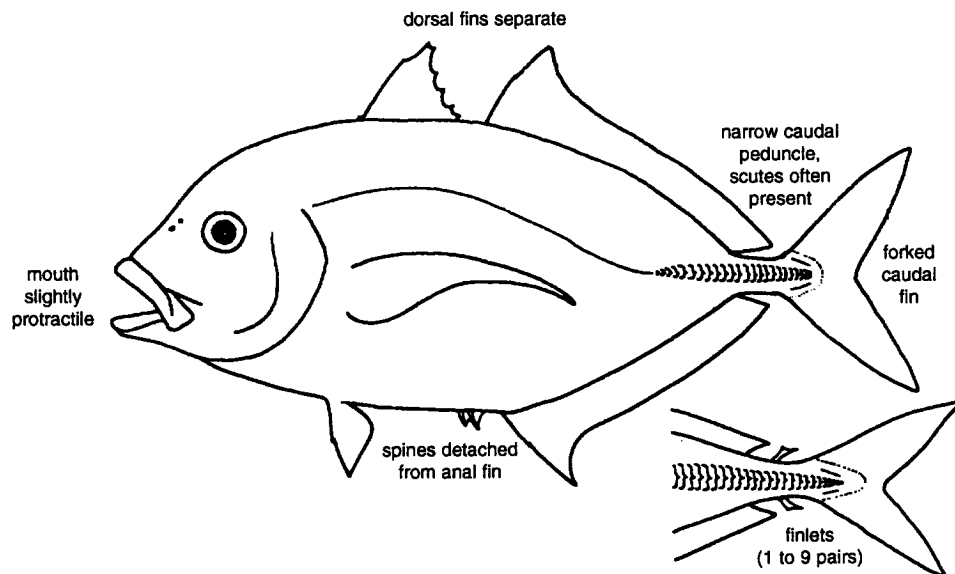


Figure 4

Diagnostic characteristics typical of the family Carangidae. From Chan et al. (1984).

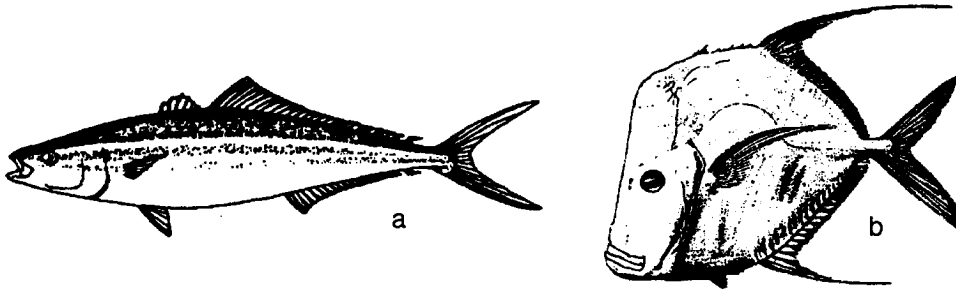


Figure 5

Variation in body shape among carangids. (a) *Elagatis bipinnulata*, (b) *Selene vomer*.
(a) From Squire and Smith (1977), (b) after Böhlke and Chaplin (1993).

spines and a posterior portion with one spine and 17 to 44 soft rays. In many carangids the last rays of the dorsal and anal fins are detached and form one to nine small posterior finlets. Pectoral fins are often long and falcate. The eye is usually protected by a transparent “adipose” eyelid, which is immovable but not fatty.

Members of the family possess small cycloid scales, which in most species are modified into a row of enlarged scutes along the posterior straight portion of the lateral line. In some carangids, particularly the genera *Carangoides* and *Caranx*, the breast is only partially scaled, and the pattern of breast squamation is useful for species identification. Body shape is generally compressed but extremely variable, ranging from slender forms like *Decapterus* and *Elagatis* to deep-bodied forms like *Selene* (Figure 5). The premaxilla is usually protrusible. Teeth range from small and villiform to large and conical, and are located variously on the premaxillae, dentary, vomer, palatines, tongue, and pharyngeals (Gunn 1990).

Distribution

Berg (1947) points out that fossil carangids are known from the Eocene, but further information on origins and dispersal could not be located. Carangids are found in all tropical and subtropical marine waters of the world, and some occur in temperate regions. Table 1 lists the various genera and number of species in each genus according to Smith-Vaniz (1984a), and the number of species found in each major geographical area as indicated in more detail by Laroche et al. (1984).

The species found in Hawai‘i are listed in Table 2. None are endemic, and all are probably derived from the Indo-West Pacific. Nine of the 24 local species are circumtropical in distribution, as indicated in Table 3. Differences in local distribution of some species has been noted anecdotally, especially between the Northwestern Hawaiian Islands (NWHI) and the main islands. *Pseudocaranx dentex* and *Carangoides ferdau* seem to be more common in the NWHI, and *P. dentex* is rarely seen in the main islands. *Decapterus tabl* is also more common in the

	No. of Species	Ind. Ocean	West Pac.	Cent. Pac.	East Pac.	West Atl.	East Atl.	Hawai'i
Trachinotini								
<i>Lichia</i>	1	1					1	
<i>Trachinotus</i>	20	5	6	2	4	5	4	
Scomberoidini								
<i>Oligoplites</i>	5				3	3		
<i>Parona</i>	1					1		
<i>Scomeroides</i>	4	4	4	1				1
Naucratiini								
<i>Campogramma</i>	1						1	
<i>Elagatis</i>	1	1	1	1	1	1	1	1
<i>Naucrates</i>	1	1	1	1	1	1	1	1
<i>Seriola</i>	9	3	5	4	3	5	4	3
<i>Seriolina</i>	1	1	1					
Carangini								
<i>Alectis</i>	3	2	2	1	1	1	2	1
<i>Alepes</i>	4	3	4					
<i>Atropus</i>	1	1	1					
<i>Atule</i>	1	1	1	1				1
<i>Carangoides</i>	22	17	18	4	3	2		3
<i>Caranx</i>	14	7	8	5	5	4	5	4
<i>Chloroscombrus</i>	2				1	1	1	
<i>Decapterus</i>	10	5	8	5	3	3	4	4
<i>Gnathanodon</i>	1	1	1	1	1			1
<i>Hemicaranx</i>	4				2	1	1	
<i>Megalaspis</i>	1	1	1					
<i>Pantolabus</i>	1		1					
<i>Parastromateus</i>	1	1					1	
<i>Pseudocaranx</i>	3	1	2	1	1	1	1	1
<i>Selar</i>	2	2	2	1	1	1	2	1
<i>Selaroides</i>	1	1	1					
<i>Selene</i>	7				3	3	1	
<i>Trachurus</i>	12	3	3		2	1	4	
<i>Ulua</i>	2	1	2					
<i>Uraspis</i>	3	3	3	2	2	1	2	2

Table 1

Worldwide distribution of carangid genera. After Laroche et al. (1984), Smith-Vaniz (1984a), and Randall (1996).

Hawaiian name, Species, Originally described as	Synonyms*, other valid names	Common name
Scomberoidini		
Lai, <i>Scomberoides lysan</i> <i>Scomber lysan</i> Forsskål, 1775	<i>Chorinemus sanctipetri</i> *	Leatherback
Naucratiini		
Kamanu, <i>Elagatis bipinnulata</i> <i>Seriola bipinnulata</i> Quoy & Gaimard, 1825		Rainbow runner
<i>Naucrates ductor</i> <i>Gasterosteus ductor</i> Linnaeus, 1758		Pilotfish
Kāhala, <i>Seriola dumerili</i> <i>Caranx dumerili</i> Risso, 1810		Greater amberjack
Kāhala, <i>Seriola lalandi</i> Valenciennes, 1883	<i>S. zonata</i> *, <i>S. aureovittata</i> *	Yellowtail
Kāhala, <i>Seriola rivoliana</i> Valenciennes, 1833		Almaco jack
Carangini		
Ul原因 kihikihi, <i>Alectis ciliaris</i> <i>Zeus ciliaris</i> Bloch, 1787	<i>Carangoides ajax</i> *	African pompano
‘Ōmaka, <i>Atule mate</i> <i>Caranx mate</i> Cuvier, 1833	<i>Alepes mate</i>	Yellowtail scad
Ul原因, <i>Carangoides equula</i> <i>Caranx equula</i> Temminck & Schlegel, 1844	<i>Kaiwarinus equula</i>	Whitfin trevally
Ul原因, <i>Carangoides ferdau</i> <i>Scomber ferdau</i> Forsskål, 1775		Barred jack
Ul原因 (papa), <i>Carangoides orthogrammus</i> <i>Caranx orthogrammus</i> Jordan & Gilbert, 1882		Island jack
Ul原因 aukea, <i>Caranx ignobilis</i> <i>Scomber ignobilis</i> Forsskål, 1775		Giant trevally
Ul原因 lā‘uli, <i>Caranx lugubris</i> Poey, 1860		Black trevally
‘Ōmilu, <i>Caranx melampygus</i> Cuvier, 1833		Bluefin trevally
Pake ul原因, <i>Caranx sexfasciatus</i> Quoy & Gaimard, 1825		Bigeye trevally
‘Ōpelu, <i>Decapterus macarellus</i> <i>Caranx macarellus</i> Cuvier, 1833	<i>Caranx pinnulatus</i> *	Mackerel scad
<i>Decapterus macrosoma</i> Bleeker, 1851		Slender scad
<i>Decapterus muroadsi</i> <i>Caranx muroadsi</i> Temmick & Schlegel, 1844		Amberstripe scad
<i>Decapterus tabl</i> Berry, 1968		Redtail scad
Ul原因 pa‘opa‘o, <i>Gnathanodon speciosus</i> <i>Scomber speciosus</i> Forsskål, 1775	<i>Scomber rim</i>	Golden trevally
<i>Pseudocaranx dentex</i> <i>Scomber dentex</i> Bloch & Schneider, 1801	<i>Charangus cheilio</i> *, <i>Caranx dentex</i>	White trevally
Akule, <i>Selar crumenophthalmus</i> <i>Scomber crumenophthalmus</i>	<i>Trachurops crumenophthalmus</i> *	Bigeye scad
<i>Uraspis helvola</i> <i>Scomber helvolus</i> Forster, 1801		Whitemouth jack
<i>Uraspis secunda</i> <i>Caranx secundus</i> Poey, 1860	<i>U. reversa</i> *	Cottonmouth jack

Table 2

Carangids found in Hawaiian waters. Hawaiian names from Pukui and Elbert (1986) and Titcomb (1972). Species names, synonyms, and other valid names according to Eschmeyer (1997). Common names based on Myers (1991), Randall (1996), and Randall et al. (1990).

Species	Distribution
Scomberoidini	
<i>Scomberoides lysan</i>	Indian Ocean, Western and Central Pacific
Naucratiini	
<i>Elagatis bipinnulata</i>	Circumtropical
<i>Naucrates ductor</i>	Circumtropical
<i>Seriola dumerili</i>	Indian Ocean, Western and Central Pacific, Atlantic
<i>Seriola lalandi</i>	Circumtropical
<i>Seriola rivoliana</i>	Circumtropical
Carangini	
<i>Alectis ciliaris</i>	Circumtropical
<i>Atule mate</i>	Indian Ocean, Western and Central Pacific
<i>Carangoides equula</i>	Indian Ocean, Western and Central Pacific
<i>Carangoides ferdau</i>	Indian Ocean, Western and Central Pacific
<i>Carangoides orthogrammus</i>	Indian and Pacific Oceans
<i>Caranx ignobilis</i>	Indian Ocean, Western and Central Pacific
<i>Caranx lugubris</i>	Circumtropical
<i>Caranx melampygus</i>	Indian and Pacific Oceans
<i>Caranx sexfasciatus</i>	Indian and Pacific Oceans
<i>Decapterus macarellus</i>	Circumtropical
<i>Decapterus macrosoma</i>	Indian and Pacific Oceans
<i>Decapterus muroadsi</i>	Western and Central Pacific
<i>Decapterus tabl</i>	Indian Ocean, Western and Central Pacific, Atlantic
<i>Gnathanodon speciosus</i>	Indian and Pacific Oceans
<i>Pseudocaranx dentex</i>	Indian Ocean, Western and Central Pacific, Atlantic
<i>Selar crumenophthalmus</i>	Circumtropical
<i>Uraspis helvola</i>	Indian and Pacific Oceans, Eastern Atlantic
<i>Uraspis secunda</i>	Circumtropical

Table 3

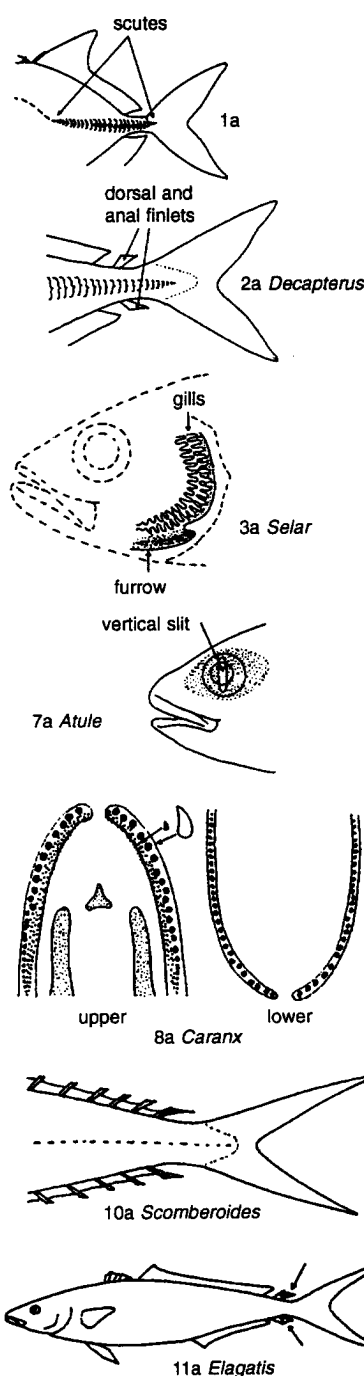
Worldwide distribution of carangids occurring in Hawaiian waters. After Laroche et al. (1984).

NWHI, especially around seamounts (Seki pers. comm.). It is unclear to what extent these variations in abundance are due to differences in fishing pressure.

A key to Hawaiian genera is given on the following page. Gosline and Brock (1960) present a key to the Hawaiian species of carangids, but it is of limited usefulness since some of the species listed have been determined not to occur in Hawaiian waters, a few of the more recently identified species are not included, and many of the generic and specific names are outdated. Meristic values for Hawaiian carangids are given in Table 4.

Key to Hawaiian genera of Carangidae

- 1a. Posterior straight part of LL with scutes; in adults, P long and falcate, in most genera longer than head (except about equal for *Selar* and shorter in some *Decapterus* spp.) 2
- 1b. No scutes on LL; P usually shorter than head (ca. 0.9-2.0 in HL) 10
- 2a. Second D and A with one or more distinctly separate finlets **Decapterus**
- 2b. Second D and A without finlets 3
- 3a. Shoulder girdle margin with a furrow ventrally, a large papilla immediately above it and a smaller papilla near upper edge **Selar**
- 3b. Shoulder girdle margin smooth 4
- 4a. In adults, spinous D entirely buried or spines short and disconnected, height of longest spine less than pupil diameter; body superficially naked, scales (where present) minute or embedded; opercle scaleless **Alectis**
- 4b. In adults, height of erect D usually longer than eye diameter and at least anterior spines united by inter-radial membrane; small scales present over most of body; opercle at least partially scaled 5
- 5a. Tongue, floor, and roof of mouth white, the rest of mouth dark **Uraspis**
- 5b. Tongue and mouth pigmentation not as above 6
- 6a. Upper and lower jaws without teeth, except a few feeble teeth in lower jaw in young **Gnathanodon**
- 6b. Jaw teeth always present, varying from 1 or 2 rows to a band of minute teeth (difficult to detect in some species of *Carangoides*) 7
- 7a. Fleshy adipose eyelid completely covering eye except for vertical slit centered on pupil; terminal ray of D and A finlet-like, a little more separated from other rays, but not detached, and about twice the length of penultimate ray **Atule**
- 7b. Fleshy adipose eyelid, if present, not as developed as above, terminal ray of D and A not finlet-like 8
- 8a. Upper jaw with an outer series of moderate to strong canines and an inner band of fine teeth; lower jaw with a single row of teeth **Caranx**
- 8b. Dentition not as above 9
- 9a. Both jaws with a band of teeth, at least anteriorly; breast naked ventrally (most species) to completely scaled **Carangoides**
- 9b. Both jaws with single series of short, conical teeth (upper jaw sometimes with an inner row of conical teeth anteriorly); breast completely scaled **Pseudocaranx**
- 10a. Base of A as long as, or only slightly shorter than, base of soft D; no C peduncle grooves, posterior D and A rays consisting of semi-detached finlets, distal 1/4 to 1/2 of rays not connected by membrane; upper lip joined to snout at midline by a bridge of skin, but crossed by a shallow groove in very young **Scomberoides**
- 10b. Base of A about 45-70% of D base length; C peduncle grooves present, dorsally and ventrally 11
- 11a. Single 2-rayed finlet behind end of D and A; maxilla ends distinctly before eye (to below front margin of eye in young) **Elagatis**
- 11b. No finlets behind D and A; maxilla ends below eye 12
- 12a. First D spines 4 or 5; A rays 15-17, cutaneous keel laterally on C peduncle well developed **Naucrates**
- 12b. First D spines 7 or 8 (anterior spines may become entirely buried in large fish); A rays 18-22; cutaneous keel laterally on C peduncle absent to moderately developed **Seriola**



Modified after Myers (1991) and Smith-Vaniz (1986a);
illustrations from Myers (1991), reprinted with permission.

Species	Dorsal fin (D)	Anal fin (A)	Gill Rakers (GR)
Scomberoidini			
<i>Scomberoides lysan</i>	VI-VII+I,19-21	II+I,17-19	3-8+15-20
Naucratini			
<i>Elagatis bipinnulata</i>	VI+I,25-28+2	I+I,18-20+2	9-10+25-26
<i>Naucrates ductor</i>	IV-V+I,25-29	II+I,15-17	5-7+16-19
<i>Seriola dumerili</i>	VII+I,29-35	II+I,18-22	5-7+14-16
<i>Seriola lalandi</i>	VII+I,30-35	II+I,19-22	8-9+18-21
<i>Seriola rivoliana</i>	VII+I,27-33	II+I,18-22	6-9+17-20
Carangini			
<i>Alectis ciliaris</i>	VI+I,18-20	II+I,15-17	4-6+12-17
<i>Atule mate</i>	VIII+I,22-25	II+I,18-21	10-13+26-31
<i>Carangoides equula</i>	VIII+I,23-25	II+I,21-24	(not available)
<i>Carangoides ferdau</i>	VIII+I,26-34	II+I,21-26	7-10+17-20
<i>Carangoides orthogrammus</i>	VIII+I,28-31	II-1,24-26	8-10+20-23
<i>Caranx ignobilis</i>	VIII+I,18-21	II+I,15-17	5-7+15-17
<i>Caranx lugubris</i>	VIII+I,20-22	II+I,16-19	6-8+17-22
<i>Caranx melampygus</i>	VIII+I,21-24	II+I,17-20	5-9+17-21
<i>Caranx sexfasciatus</i>	VIII+I,19-22	II+I,14-17	6-8+15-19
<i>Decapterus macarellus</i>	VIII+I,31-36+1	II+I,27-30+1	10-13+34-38
<i>Decapterus macrosoma</i>	VIII+I,33-38+1	II+I,27-30+1	10-12+34-38
<i>Decapterus muroadsi</i>	VIII+I,29-33+1	II+I,24-28+1	12-14+37-39
<i>Decapterus tabl</i>	VIII+I,30-31+1	II+I,24-25+1	11-12+30-32
<i>Gnathanodon speciosus</i>	VII+I,18-20	II+I,15-17	8-9+19-22+27-30
<i>Pseudocaranx dentex</i>	VIII+I,25-26	II+I,21-22	11-14+24-26
<i>Selar crumenophthalmus</i>	VIII+I,24-27	II+I,21-23	9-12+27-31
<i>Uraspis helvola</i>	VIII+I,27-30	II+I,20-22	6-7+14-15
<i>Uraspis secunda</i>	VIII+I,27-32	II+I,19-23	(not available)

Table 4

Meristic values for Hawaiian carangids. Based on Masuda et al. (1984), Smith-Vaniz (1984b), and Myers (1991).

Reproduction

Carangids are gonochoristic, and for the most part there is no apparent difference between the sexes. However, sexual dichromaticism has been described by Talbot and Williams (1956) and von Westernhagen (1974) in *Caranx ignobilis*, in which males appeared to be darker than females. Clarke and Privitera (1995) noted the soft portion of the anal fin of male *Selar crumenophthalmus* was dark black during spawning season, but white in females. Clarke (1996) observed size differences between male and female *Atule mate*, as described below.

Male carangids have no intromittent organ, and fertilization is external. Females are oviparous and iteroparous. Some species spawn pelagically, whereas others spawn close to shore. Spawning seasons for most species are fairly long, generally peaking during summer months.

Actual spawning in the wild has been described for only a few species, but seems to occur repeatedly and periodically (Thresher 1984).

Caranx

Munro et al. (1973) report capturing ripe black trevallies (*Caranx lugubris*) in the Caribbean from February through September. Sudekum et al. (1991) estimated sex ratio, spawning season, and size at first reproduction for the bluefin trevally, or 'ōmilu (*C. melampyus*), and the giant trevally, or ulua aukea (*C. ignobilis*), in relatively unexploited waters of the Northwestern Hawaiian Islands. In both species, the sex ratio was slightly skewed to females, with male:female ratios of 1:1.148 for *C. melampyus* and 1:1.39 for *C. ignobilis*. Spawning season was defined as the period of the year in which a significant proportion of fish had high gonadosomatic index (GSI) values, where $GSI = (\text{gonad wet weight} / \text{whole body wet weight}) \times 100$.

In *C. melampyus*, gravid females were found from April to November, and from May through July more than half were gravid, with June and July being peak months. A summer peak was also observed in *C. ignobilis*. Female *C. melampyus* appeared to reach sexual maturity at about 350 mm standard length (SL), and female *C. ignobilis* at about 600 mm SL. From the derived growth curves (see below), this corresponds to an age at first reproduction of about two years for *C. melampyus* and four years for *C. ignobilis*. (Note that in Hawaiian waters the current minimum size for all species of ulua and pāpio (generally defined as ulua under ten pounds) is seven inches total length, or 178 mm, for home consumption.) Fecundity was estimated for *C. melampyus* and ranged from 49,700 mature ova for a fish of 760 g (328 mm SL) to 4,270,000 for a fish of 6,490 g (640 mm SL). The authors suggest both species may reproduce for at least four to six years.

Williams (1965) noted that during the summer spawning season he sampled shoals of *C. ignobilis* in which either only males or females were caught, and suggested the sexes segregate during the prespawning period. The catch data by Sudekum et al. (1991) supported this to some extent, and was interpreted to mean that spawning is coordinated in space and time, and that large numbers of males and females aggregate to spawn. These authors further suggest that multiple clutches may be developed over the course of a year.

von Westernhagen (1974) described spawning in *C. ignobilis*. Groups of sometimes more than 100 individuals would gather close to shore, then break up into smaller groups of three to four, and descend to two or three meters above the bottom. Males were easily recognized by their black and white head region and black dorsal surface. Eventually one male would pair up with a female, the two would sink to just above the bottom, and slowly swim around each other. While circling, they were observed to release eggs and sperm into the water, during which time they could be easily approached.

Thresher (1984) notes that the only other species of *Caranx* for which spawning has been observed is the bigeye trevally (*C. sexfasciatus*). A pair of fish in a 22.5 m by 7.6 m enclosure were seen in late afternoon to swim faster than other fish in the school, approach each other closely, and press their ventral surfaces together for some time, with one fish maintaining an almost horizontal position.

Atule

Watson and Leis (1974) showed that yellowtail scad, or 'ōmaka (*Atule mate*), spawn in Hawaiian waters between late spring and early fall, and spawning primarily occurs within partially enclosed bays. Clarke (1996) determined the spawning season in Kane'ōhe Bay, O'ahu to extend from March through October, with some eggs present as late as December. He found newly spawned 'ōmaka eggs in samples collected as early as 0800, and present until 1300, indicating 'ōmaka spawn in the morning. These eggs were mostly found in open areas of the bay where bottom depth was at least 10 m. Size at maturity was estimated at 150 to 160 mm. Batch fecundity of females 188 to 232 mm SL ranged from 63,000 to 161,000 ova, and for a female of average weight (155 g) was estimated at about 115,000 eggs.

Sex ratios in this study were skewed, with males making up over two-thirds of the fish collected, which was interpreted to suggest segregation by sex and differential movement into the bay. In addition, captured males were routinely considerably larger than females, which the authors interpreted as evidence that males may have higher growth rates or lower mortality rates than females.

Gnathanodon

A limited amount of information regarding the golden trevally, or ulua pa'opa'o (*Gnathanodon speciosus*), was obtained by Watson and Leis (1974) from studies in Kane'ōhe Bay. Newly spawned eggs were collected in the bay from late February through mid-October, with a peak from late April through early September. Five peaks of egg abundance were noted at approximately one-month intervals, and peaks seemed to coincide with the first and third quarters of the moon. Pa'opa'o appeared to begin spawning in the early evening hours and continue for some hours into the night.

Decapterus

Of the four species of *Decapterus* found in Hawaiian waters, the mackerel scad, or 'ōpelu (*D. macarellus*), is by far the most common. Spawning takes place in shallow (20 to 100 m) inshore waters from April through August, peaking in May through July. Females have been reported to spawn only once a season (DLNR 1979); however, that would not seem to be consistent with what is known about spawning frequency in most of the rest of the family.

Size at maturity is estimated at 245 mm SL for both males and females. Batch fecundity of females 248 to 300 mm SL ranged from 13,000 to 236,000 ova (Clarke and Privitera 1995).

Studies by Widodo (1991) on the locally occurring congener *D. macrosoma* in the Java Sea indicated a size at maturity of 148 mm for males and 155 mm for females. In the Philippines, *D. tabl* spawns somewhat later than *D. macarellus*, and batch fecundity ranges from 28,700 to 48,700 eggs (Shiota 1986b).

Selar

The spawning season for bigeye scad, or akule (*Selar crumenophthalmus*), in Hawaiian waters has been given variously as April through November (Kawamoto 1973), February through August (DLNR 1979), and April through October (Clarke and Privitera 1995). The latter authors note that there appears to be some annual variation in season, and spawning seems to take place between dawn and dusk. Akule form large schools in shallow, flat-bottomed waters during the spawning season, and are believed to be Hawai'i's most abundant carangid (DLNR 1979).

Size at first maturity is estimated by Clarke and Privitera (1995) at 190 to 200 mm SL. Batch fecundity of females 199 to 256 mm SL ranged from 48,000 to 262,000 eggs. Individual females apparently spawned about every three days.

Seriola

Kikkawa and Everson (1984) give the size at maturity in greater amberjack, or kāhala (*Seriola dumerili*), females as 72 cm FL, with a spawning season from February through June peaking in March and April. Batch fecundity estimates ranged from 1.3 to 4.0 million eggs for fish 83.0 to 118.6 cm FL.

Marino et al. (1995) collected wild *S. dumerili* in the South Mediterranean Sea during the 1990-1992 spawning seasons. Maturing ovaries were present in 53.9% of four-year-old females, and spermatozoa were found in deferent ducts in 80% of four-year-old males. They concluded that the first reproductive season was four years of age for both sexes, although 40% of males were sexually mature at three years. The median length at which 50% of fish attained sexual maturity was estimated at 109 cm SL in males and 113 cm SL in females. All fish at least 128 cm SL were sexually mature.

The spawning period had been considered to peak between late May and mid-July in those waters, but observations of mature ovaries supported a longer spawning season. Post-ovulatory follicles were found in some maturing ovaries, and their presence was interpreted to indicate *S. dumerili* may release batches of eggs in several waves during the same spawning season. Thompson and Munro (1974) note that ripe *S. dumerili* and *S. rivoliana* have been collected in the Caribbean as late as November. They also cite reports of ripe ovaries in large *S. dumerili* that occupied over one-third of the abdominal cavity, and were estimated to contain over a million eggs.

Elagatis

Rainbow runners, or kamanu (*Elagatis bipinnulata*), spawn throughout the year, and peak around March. The larvae are described as the most abundant of the epipelagic carangids (Seki 1986a).

Early Life History

Carangid eggs range in diameter from about 0.7 to 1.3 mm, and are generally transparent and spherical with a segmented yolk, narrow perivitelline space and one to several oil globules, often with melanophores (Figure 6). They are difficult to distinguish from eggs of many other families of marine fishes. Hatching commonly occurs 24 to 48 hours after spawning, depending on egg size and water temperature. However, Watson and Leis (1974) found that eggs of ulua pa'opa'o (*Gnathanodon speciosus*) hatch after 18 hours.

At hatching, carangid larvae are usually 1.0 to 2.0 mm notochord length (NL), and the yolk sac is fairly large. Notable characteristics of yolk sac larvae include an oil globule at the anterior yolk sac ventral to the head, and the presence of 24 to 27 myomeres, but for the most part newly hatched larvae are also difficult to identify and distinguish from those of many other marine fishes (Leis and Trnski 1989). Within a day after hatching the gut develops as a straight tube, and a single gut loop forms after about five days, when larvae are 3 to 4 mm NL. The lengths and times at which this occurs vary somewhat with species (Figure 7).

The oil globule and yolk sac are absorbed by 72 hours after hatching (Venkataramanujam and Ramamoorthi 1983). Following absorption, which occurs at 2.0 to 4.0 mm NL, larval carangids vary in shape from relatively slender forms with body depth (BD) 20 to 27% SL to more deep bodied forms with BD 32 to 59% SL. In general, carangid larvae have large heads and are deeper bodied than those of many other marine fishes. They become more recognizable on the basis of body shape, presence of 24 myomeres for all Hawaiian species (except *Scomberoides*,

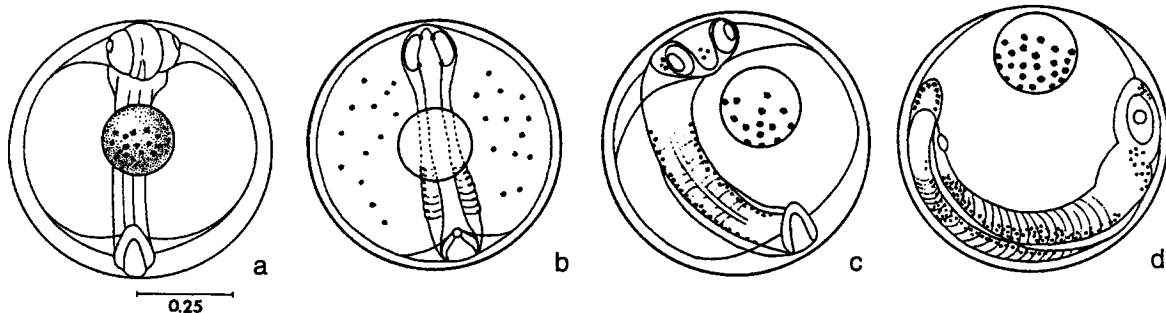


Figure 6

(a) Generalized carangid egg. (b-d) Development of egg of 'ōmaka, *Atule mate*: (b) early middle stage, (c) advanced middle stage, (d) early late-stage. (a) From Watson and Leis (1974), (b-d) from Miller and Sumida (1974).

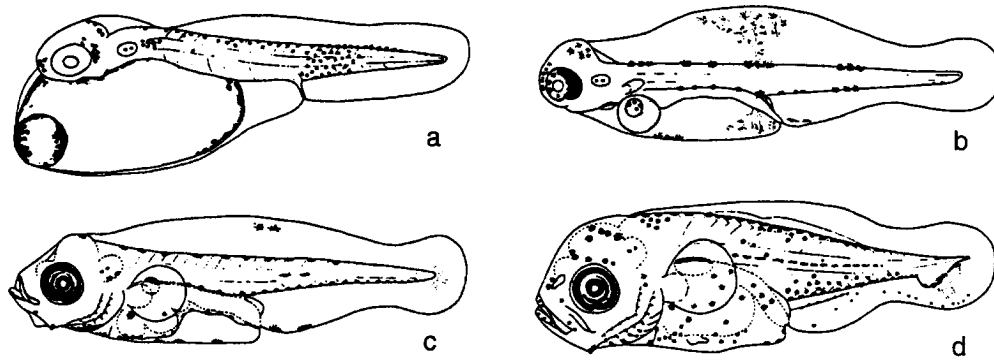


Figure 7

Larval development in *Atule mate*. (a) just after hatching, 1.62 mm SL; (b) three days old, 2.26 mm SL; (c) six days old, 3.06 mm SL; (d) twelve days old, 3.96 mm SL. From Miller and Sumida (1974).

which has 26), long preopercular spines (except *Atule mate*), dorsal crest (again except *A. mate*), and midline melanophores. Identification of species is difficult, since major characteristics are usually differences in pigmentation which change with development (Miller et al. 1979).

The formation of head spines occurs fairly early, at about the same time as yolk sac absorption. The first to appear is a preopercular spine at the angle of the posterior margin of the preopercle, and its size and shape are useful in distinguishing genus. A series of spines develops along the posterior margin, and a second series develops along the anterior margin. The number of spines increases through preflexion, flexion, and postflexion stages to a maximum of about 9 anterior and 11 posterior, and does not appear to be constant for a particular species. Numbers of spines decrease as the larva transforms into the early juvenile stage, and eventually spines become overgrown by tissue and bone.

In many species a median supraoccipital crest develops on the head during preflexion. Its presence is useful in distinguishing carangid larvae from those of other fishes, since it doesn't occur in larvae of most other fish families. The crest persists until late in transformation when it also becomes overgrown by bone and tissue. Supraocular spines and serrations develop in larvae from a number of carangid genera, and supracleithral spines develop in all species (Figure 8).

At the time of hatching, dorsal, preanal, anal, and caudal finfolds are already present. The pectoral fin base and finfold develop in yolk-sac larvae. Fin formation generally proceeds sequentially from caudal, pectoral, anal and soft dorsal, spinous dorsal, to pelvic, with the dorsal and anal fins developing anterior to posterior. Completion of dorsal and anal fin rays occurs in conjunction with or shortly after flexion.

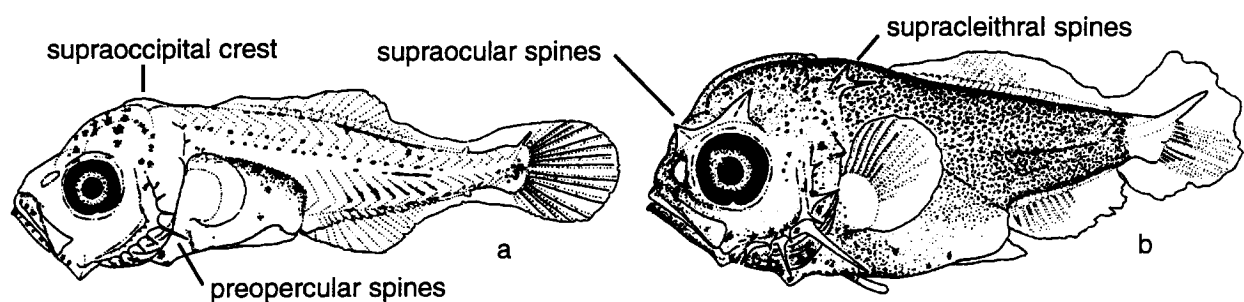


Figure 8

Supraoccipital crest, and preopercular, supraocular, and supracleithral spines in carangid larvae. (a) *Selar crumenophthalmus*, 5.6 mm; (b) *Naucrates ductor*, 4.7 mm. After Laroche et al. (1984).

Ossification of dorsal and anal fin spines occurs proximally from the distal tip in many species. The two anteriormost anal fin spines are separated by a gap from the third spine once the fins have formed, and this is an important distinguishing characteristic unique to carangids. Most species develop an antrose spine on the anterodorsal margin of the first dorsal fin pterygiophore, which is obvious in larvae and juveniles but eventually becomes covered with skin.

Pigmentation is variable in carangid larvae, and its diagnostic usefulness is limited. In general, rows of melanophores appear along the dorsal and ventral margins of the tail by late preflexion, then on the head over the brain. Also during preflexion a row of small melanophores develops along the lateral midline, which persists into the juvenile stage. This is sometimes referred to as a “lateral line streak.”

Laroche et al. (1984) describe developmental osteology in some detail, and elaborate on distinguishing characters useful in identifying flexion and postflexion carangid larvae to the genus level.

Scales begin to form during transformation to the juvenile stage, and in many species scutes develop as modified scales along the posterior portion of the lateral line. Scale development proceeds anteriorly, dorsally, and ventrally from the region of the lateral line anterior and adjacent to the caudal peduncle. Except as noted, most of the generalized information about early life history in carangids presented above is based on Laroche et al. (1984).

Very little information is available concerning larval behavior. Cha et al. (1994) sampled fish larvae off the Florida keys and found 92.4% of carangid larvae occurred in the upper 25 m of the water column, and 100% occurred in the upper 50 m.

Development from larval through juvenile toward adult stages proceeds rather directly in carangids, and adult characters are gradually acquired. There are no sudden developmental rate

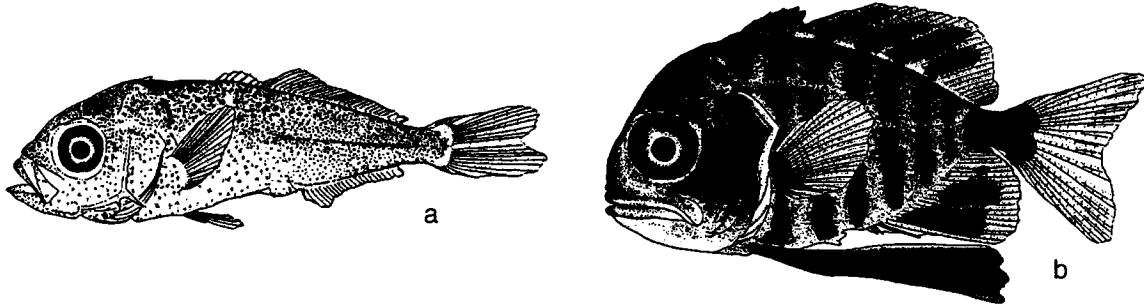


Figure 9

(a) Late postflexion larva of *Elagatis bipinnulata* (11.4 mm), (b) small juvenile of *Uraspis secunda* (25.6 mm). After Laroche et al. (1984).

changes between stages. By late postflexion, at a size of 8 to 9 mm, larvae are recognizable as small carangids (Figure 9a), and Berry (1959) considers transformation from larva to juvenile to occur at about 8 mm SL. Juveniles develop spotted or barred patterns at 15 to 20 mm SL (Figure 9b), and these pigmentation patterns persist until the fish is 100 to 200 mm SL, depending on species.

Leis (1991) indicates that carangid fishes do not settle. Young juveniles often associate with floating or drifting objects, including jellyfish, clumps of algae, flotsam, etc. As they grow larger, they tend to lose the banded pattern and move inshore, where they often take up a schooling existence. Migration to inshore waters seems to occur when the fish are 21 to 50 mm SL (Berry 1959). Some forms, such as the pilotfish (*Naucrates ductor*) and golden trevally (*Gnathanodon speciosus*) do not lose the banded pattern. *Naucrates* juveniles apparently do not move inshore; as they grow, they continue to accompany larger objects, including sharks and other large carnivorous fishes (Böhlke and Chaplin 1993).

A number of authors note that the young of many carangid species are known to enter estuaries. Blaber and Cyrus (1983) studied this phenomenon in estuaries of Natal, South Africa, in several species which also occur in Hawai'i. The following summaries are from their work.

Caranx ignobilis juveniles were captured in estuaries at sizes of at least 40 mm. Juveniles could tolerate salinities of 1.5 to 38‰, and subadults from 0.5 to 35‰. Juveniles below 200 mm would occur in highly turbid waters. Recruitment into estuaries occurred during the austral summer, but larger fish were present throughout the year.

C. melampygus juveniles were also captured at sizes of at least 40 mm. Those below 170 mm tolerated salinity ranges from 6.0 to 35‰, and those above 170 mm were found in waters from 8.0 to 35‰. Juveniles were found only in clear waters, and recruitment occurred from October through March.

Recruitment of *C. sexfasciatus* into estuaries occurred from October through April, when fish were from 30 to 60 mm. All sizes tolerated water from 0.5 to 40‰, and juveniles below 120 mm were found in waters of varying turbidity.

Scomberoides lysan fry entered estuaries during the late austral summer, from January through April, at sizes of 20 to 30 mm. Juveniles tolerated salinity ranges of 6.5 to 35‰, and subadults from 0.5 to 35‰. All size classes were found in water of low turbidity. Gosline and Brock (1960) note that in Hawai'i, juveniles of one to four inches in length are often found in shallow brackish water.

Recruitment of *Atule mate* in Hawaiian waters may be a fairly straightforward process, since the eggs are spawned in bays, which is also a preferred habitat of adults. Gosline and Brock (1960) state that juveniles under one inch in length are often found under jellyfish.

Age and Growth

Carangids are noted for the changes they undergo with growth (Böhlke and Chaplin 1993), and these changes have likely been responsible for misidentification of specimens and contributed to some of the general taxonomic confusion that has occurred. In the case of *Uraspis helvola*, for example, fish below 150 mm SL possess both anterior and posterior retrose scutes and middle antrose scutes, but in larger fish the antrose scutes have gradually transformed and only retrose scutes are present. Other changes that take place as the fish passes 150 mm SL are found in dentition, pectoral fin length, and pelvic fin length and shape, in addition to changes in banding pattern as described above (Reuben 1968).

An interesting example of change with growth occurs in juveniles of the African pompano, or ulua kihikihi (*Alectis ciliaris*), which are easily recognized by the presence of long filaments trailing from the first four or five rays of the dorsal and anal fins. These filaments may be twice the length of the body, and as the fish gets larger they gradually shorten and eventually disappear. It has not been determined what exactly happens to them, or their possible function. Randall et al. (1990) and Myers (1991) speculate the filaments may serve to mimic the stinging tentacles of jellyfishes for protection from predators.

‘Ōpelu (*Decapterus macarellus*) grow to about 20.0 cm in 12 months, 27.1 cm in 24 months, and 30.7 cm in 36 months (cited by Shiota 1986a). Akule (*Selar crumenophthalmus*) grow to about 22.9 cm in 12 months and 30.5 cm in 24 months (Shiota 1986c).

von Bertalanffy growth equations could be found for a few local species, and are given in Table 5. Watarai (1973) describes the growth of juvenile ‘ōmaka by the equation $Y = (2.29) X^{6.61 \times 10^{-1}}$ and of adult ‘ōmaka by $Y = (143.05) e^{3.45 \times 10^{-4} X}$, where Y is calculated

Species	Growth Equation
<i>Caranx ignobilis</i> ¹	$L_t = 1838 (1 - e^{-0.111(t - 0.097)})$
<i>Caranx melampygus</i> ¹	$L_t = 897 (1 - e^{-0.233(t + 0.044)})$
<i>Selar crumenophthalmus</i> ²	$L_t = 270 (1 - e^{-0.215(t + 0.333)})$
<i>Uraspis helvola</i> ³	$L_t = 633 (1 - e^{-0.214(t + 1.213)})$
<i>Elagatis bipinnulata</i> ⁴	$L_t = 930.2 (1 - e^{-0.214(t + 0.449)})$
<i>Seriola dumerili</i> ⁵	$L_t = 149.3 (1 - e^{-0.314(t - 0.0420)})$

Table 5

Von Bertalanffy growth equations for some local carangids. From: 1 - Sudekum et al. (1991), 2 - Kawamoto (1973), 3 - Chiou and Chen (1993), 4 - Iwasaki (1995), 5 - Humphreys (1986).

Species	Length-Weight Relationship
<i>Caranx ignobilis</i> ¹	$W = 2.30 \times 10^{-5} (SL)^{2.977}$
<i>Caranx melampygus</i> ¹	$W = 2.86 \times 10^{-5} (SL)^{2.974}$
<i>Pseudocarnax dentex</i> ²	$W = 1.70 \times 10^{-8} (FL)^{3.0074}$
<i>Selar crumenophthalmus</i> ³	$W = 1.80 \times 10^{-6} (FL)^{3.397}$
<i>Elagatis bipinnulata</i> ⁴	$W = 2.32 \times 10^{-4} (FL)^{2.24}$
<i>Seriola dumerili</i> ⁵	$W = 2.21 \times 10^{-8} (FL)^{2.9412}$

Table 6

Length-weight relationships for some local carangids. From: 1 - Sudekum et al. (1991), 2 - Seki (1986b), 3 - Kawamoto (1973), 4 - Seki (1986a), 5 - Humphries (1986).

length in mm for a given day (X). He does not give a von Bertalanffy equation. Growth curves for certain species are shown in Figure 10.

Length-weight relationships were also found for some local species, and are given in Table 6. Watarai gives the equation for juvenile 'ōmaka as $Y = (2.01 \times 10^{-5}) X^{3.02}$, and for adults as $Y = (7.68) e^{1.43 \times 10^{-2} X}$, where Y is apparently wet weight in grams and X length in mm. Length-weight curves for certain species are shown in Figure 11.

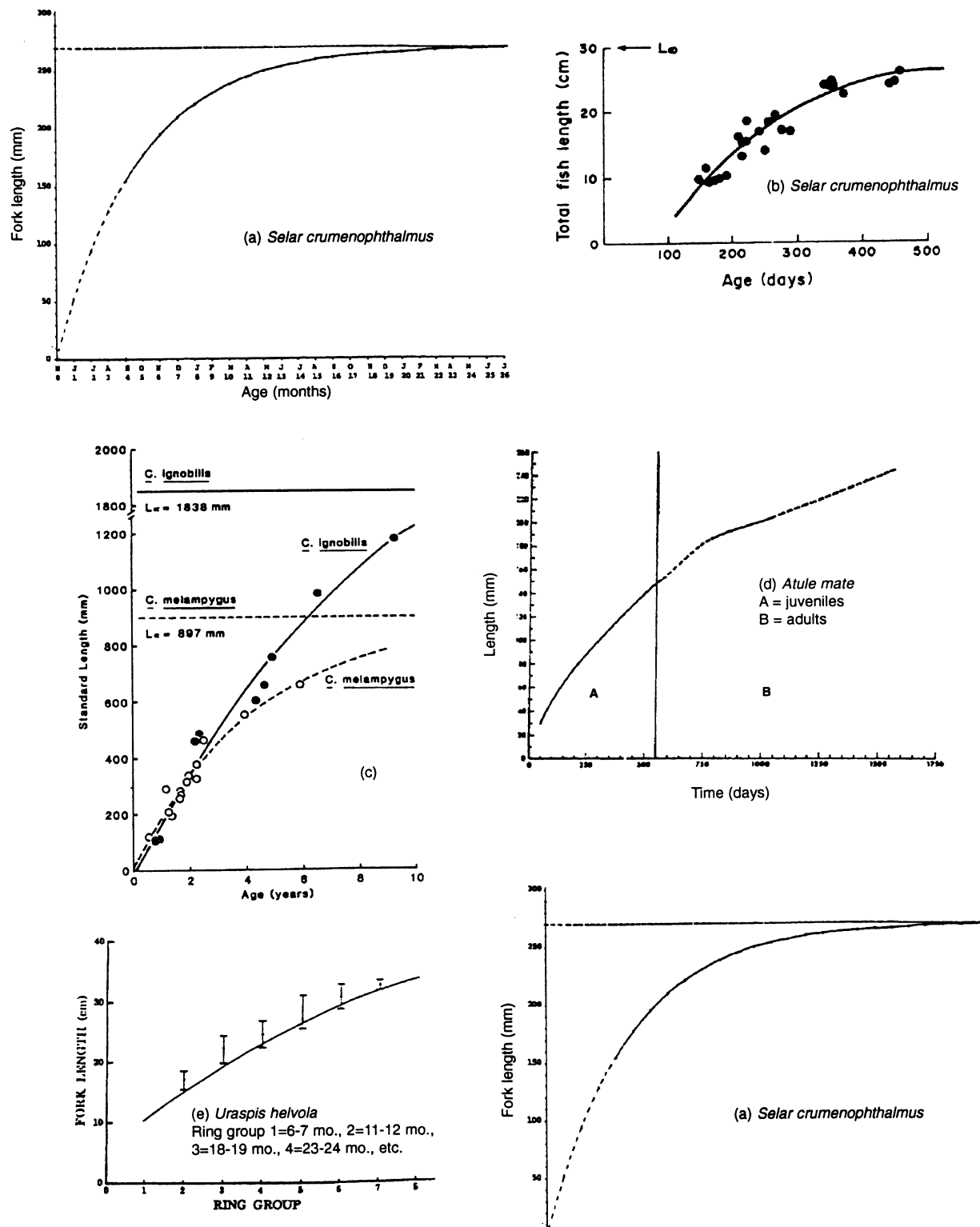


Figure 10

Growth curves for six Hawaiian carangids. (a) From Kawamoto (1973), (b) from Dalzell and Peñafior (1989), (c) from Sudekum et al. (1991), (d) from Watarai (1973), (e) from Chiou and Chen (1993), (f) from Iwasaki (1995).

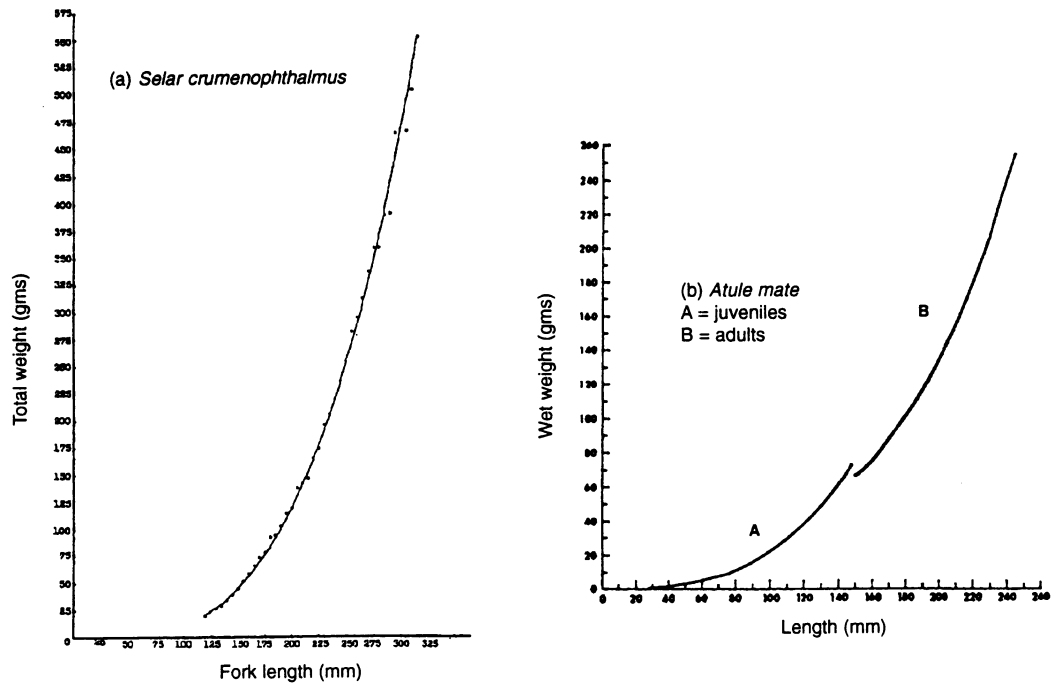


Figure 11

Length-weight curves for two Hawaiian carangids. (a) From Kawamoto (1973), (b) from Watarai (1973).

Sudekum et al. (1991) conducted maximum feeding rate experiments on *Caranx ignobilis* and *C. melampygus*, in which the fish were fed *ad libitum* at least three times per day during several periods ranging from four to ten consecutive days each. *C. melampygus* grew from an average of 174 mm SL to 239 mm SL over 161 days, for an average growth rate of 0.40 mm/day, as compared with an instantaneous growth rate of 0.45 mm/day calculated from the von Bertalanffy growth curve. Mean weight increased from 124.5 g to 302.5 g over the same period. (Results for *C. ignobilis* were not given, because the fish seemed to be in poor health during the experiment.) These authors also provided the only set of otolith data (for the same two species) that could be found.

Maximum sizes attained by species found in Hawaiian waters are given in Table 7.

Species	Length, Weight	Hawai'i Record (kg)
Scomberoidini		
<i>Scomberoides lysan</i>	to 70 cm FL	2.4 (5 lbs 4.6 oz)
Naucratiini		
<i>Elagatis bipinnulata</i>	to 115 cm FL, 15.3 kg	14.1 (30 lbs 15 oz)
<i>Naucrates ductor</i>	to 70 cm TL	
<i>Seriola dumerili</i>	to 188 cm, 80.6 kg	55.0 (121 lbs*)
<i>Seriola lalandi</i>	to 193 cm, 58 kg	
<i>Seriola rivoliana</i>	to 110 cm FL, 24 kg	
Carangini		
<i>Alectis ciliaris</i>	to 80 cm FL, 18.8 kg (Atlantic)	21.8 (48 lbs)
<i>Atule mate</i>	to 34 cm FL	
<i>Carangoides equula</i>	to 37 cm	
<i>Carangoides ferdau</i>	to 70 cm, 8.0 kg (S. Africa)	
<i>Carangoides orthogrammus</i>	to at least 71 cm FL, 6.1 kg	7.7 (17 lbs 1.2 oz)
<i>Caranx ignobilis</i>	to at least 165 cm FL, 68 kg	86.8 (191 lbs)
<i>Caranx lugubris</i>	to 91 cm FL, 15.5 kg	
<i>Caranx melampygus</i>	to at least 80 cm FL, 7 kg	10.2 (22 lbs 6.5 oz)
<i>Caranx sexfasciatus</i>	to 85 cm FL	7.1 (15 lbs 8.8 oz)
<i>Decapterus macarellus</i>	to 35 cm SL	1.4 (3 lbs 2.6 oz*)
<i>Decapterus macrosoma</i>	to 35 cm FL	
<i>Decapterus muroadsi</i>	to 50 cm FL	
<i>Decapterus tabl</i>	to 50 cm	
<i>Gnathanodon speciosus</i>	to 110 cm, 14.8 kg (S. Africa)	7.4 (16 lbs 3 oz)
<i>Pseudocaranx dentex</i>	to 96 cm	
<i>Selar crumenophthalmus</i>	to 30 cm FL	0.9 (1 lb 15.5 oz)
<i>Uraspis helvola</i>	to 46 cm FL	
<i>Uraspis secunda</i>	to 48 cm	

Table 7

Maximum sizes of carangids found in Hawaiian waters. After Smith-Vaniz (1986a), Smith-Vaniz et al. (1990), Myers (1991). Hawai'i records from C. Johnston, Hawai'i Fishing News (pers. comm.).

*Not identified to species, reported as k hala and  opelu only.

Feeding

Carangids are generally described as fast-swimming carnivores and pursuit predators. Randall (1967) divides the family by diet into fish-feeders and plankton-feeders, although that is somewhat over-simplified. The planktivores include the genera *Atule*, *Decapterus*, and *Selar*. *A. mate* feeds diurnally on small fish and crustaceans, and is described by Gosline and Brock (1960) as a "voracious plankton feeder." *D. macarellus* feeds largely on hyperiid amphipods and crab megalops, along with fish larvae. *D. tabl* feeds in the water column on copepods, crustacean mysids, and small fishes (Shiota 1986a, 1986b).

The diet of *S. crumenophthalmus* includes small fishes (esp. anchovies and holocentrids) and crustaceans such as stomatopods, copepods, shrimps, and crab megalops taken mostly by night

from the water column. Juveniles apparently feed by day, at least to some extent (Shiota 1986c).

Diet and feeding behavior in *Caranx ignobilis* has been fairly well studied in Hawai‘i. Sudekum et al. (1991) found their diet to consist of parrotfish, ‘ōpelu, wrasses, bigeyes, eels, cephalopods (both squid and octopus), and crustaceans (lobsters, crabs, and shrimp). The diet indicates *C. ignobilis* feeds nocturnally at least part of the time, and forages in both shallow water reef areas and open water habitats. *C. ignobilis* is one of the few fishes known to eat large lobsters, and it has been observed feeding on undersized and berried lobsters released from commercial fishing vessels.

Major (1978) studied predation behavior by small (212 to 245 mm SL) *C. ignobilis* on Hawaiian anchovies, or nehu (*Stolephorus purpureus*), at Coconut Island, O‘ahu. He described the jack as a facultative schooling species, schooling temporarily for feeding or reproduction but not as a requirement for survival. He also considered it to be an opportunistic carnivore, feeding by day and night on fish and crustaceans, with nocturnal feeding occurring mostly in the early evening.

Major’s study involved interactions between young jacks (pāpio) singly or in small groups with nehu schools of various sizes. Single predators were most successful at capturing isolated prey, and had difficulty capturing schooled prey, perhaps because of the amount of time required to identify and align themselves with an individual prey item for a successful strike.

When pāpio were allowed to hunt as a small group (three to five individuals), they had more success with schooled prey. If the group formed prior to interacting with the nehu, there would usually be a lead pāpio with others following. The leader would often charge the school as if it were hunting individually, and the following pāpio would seem to key in on the activity of the leader. The leader may have been orientating to individual prey items that the other pāpio did not see. Orientations to the prey were mostly directed at individuals that seemed to make mistakes, such as moving too far away from the school to snap at something in the water, turning the wrong way when the school changed directions, or falling behind or moving too far ahead of the school. In general, the marginal or peripheral nehu were the ones most likely to be attacked.

In some instances the pāpio groups would bunch together and form an inverted “V” that would rapidly penetrate the nehu school. The penetration would break up the school, usually causing some prey to become isolated. Before these isolated nehu could rejoin the school, they would be attacked. This ability to break up prey schools was considered to be a major benefit of grouping by predators. Parrish (1993) also noted increased predatory success by jacks (*C. caballus*) when hunting in groups of three to five, especially when breaking up schools and ori-

enting to stragglers and “pseudopods” (groups that briefly detach from the school and then reintegrate).

Major also made observations regarding handling times by pāpio. Often prey were engulfed and swallowed nearly simultaneously. But sometimes they were caught by the head or tail, or crossways between the pāpio’s jaws, and had to be manipulated before swallowing. The pāpio would then spit the prey out, swim at it again, and engulf it. Sometimes a number of such expulsions would be required before the pāpio was successful. While the prey was being manipulated in this way, it was accessible to other predators. If other pāpio were present, they would often break off their own interactions with prey and chase and snap at portions of the nehu sticking out of the mouth of the other pāpio, usually with limited success.

Potts (1980) studied predatory behavior in *C. melampygyus* in the Indian Ocean. He described the species as a diurnally active predator with increased activity at dawn and dusk when small midwater planktivorous fishes are moving to or from the shelter of the reef. From his observations, it appeared *C. melampygyus* usually hunted singly or in pairs, but sometimes in small groups. In Hawaiian waters, single or small groups of ‘ōmilu are often seen following closely behind groups of the blue goatfish, or moano kea (*Parupeneus cyclostomus*), perhaps to capture prey driven out by the goatfish (Hobson 1974, pers. obs.).

Sudekum et al. (1991) note some apparent ontogenetic shift in the diet of ‘ōmilu. Smaller individuals seem to take a higher incidence of crustaceans. Larger fishes feed on wrasses, goatfish, damselfish, parrotfish, and filefish. The lack of deep-water species suggests *C. melampygyus* feeds mostly in reef areas, and the low incidence of nocturnally active prey indicates it is probably a diurnal or crepuscular predator.

Blaber and Cyrus (1983) found that juvenile *C. sexfasciatus* below 200 mm were primarily piscivorous on fry of estuarine species, but a large part of the diet consisted of penaeid shrimps. *C. sexfasciatus* above 200 mm were almost entirely piscivorous, but Myers (1991) describes them as nocturnal feeders on small fishes and crustaceans.

C. lugubris feeds primarily on other fishes (Smith-Vaniz 1986b), but little else is known about its feeding behavior. Longhurst and Pauly (1987) state that shoals of *Caranx* often feed at the surface and form “feeding flurries” by forcing shoals of small fish to the surface, but they do not elaborate about the species and no other reference to that effect could be found.

The island jack (*Carangoides orthogrammus*) is sometimes seen “rooting” in the sand for crustaceans and fishes (Myers 1991). No other information regarding feeding in this or the other two locally occurring *Carangoides* species could be located.

The white trevally (*Pseudocaranx dentex*) is described as an opportunistic carnivore. Its diet includes mainly fishes like conger eels, bigeyes, and groupers, but also octopuses, and crustaceans such as crabs and shrimps. This indicates a range of foraging grounds, including near the bottom in deeper offshore waters (Seki 1984, 1986d).

Adult kamanu (*Elagatis bipinnulata*) feed on invertebrates, especially crustaceans, and small fishes. Postlarvae and juveniles eat mostly calanoid copepods and *Corycaeus* (Seki 1986a)

The pilotfish (*Naucrates ductor*) is well known for its commensal relationship with sharks, rays, and other large fishes. It feeds on scraps of the host's food, along with small fishes and invertebrates, and may eat ectoparasites from the host's body (Smith-Vaniz 1986b).

Humphreys (1986) notes that as kāhala (*Seriola dumerili*) increase in size their diet consists of a larger proportion of *Decapterus*. He also mentions dietary differences between the Northwestern Hawaiian Islands (NWHI) and the main islands. In the NWHI the main dietary components are octopus and other bottom-associated prey (Humphreys and Kramer 1984), but in the main islands the diet is predominantly *Decapterus* and other prey from the water column.

Badalamenti et al. (1995) describe ontogenetic shifts in the diet of *S. dumerili* in the Mediterranean. Individuals up to 80 mm SL feed mostly on copepods and crustacean larvae. Fish from 80 to 120 mm SL represent a transition stage in which zooplankton are still eaten, along with some benthic and nectonic organisms like pipefishes and seahorses associated with seagrass systems. Individuals above 120 mm SL feed mainly on nectonic and nectobenthic items such as goatfishes and porgies.

Grau et al. (1992) point out that the large number of pyloric caeca between the stomach and large intestine of *S. dumerili* is consistent with a diet of large prey. Sanderson et al. (1996) analyzed a videotape of *S. dumerili* displaying what appeared to be ram suspension feeding behavior in the field. An individual was observed swimming in a tight circular pattern around a reef with an open mouth and abducted opercula, and periodically closing its mouth in a manner similar to that of suspension-feeding fish. Because the fish was not captured, its stomach contents could not be analyzed to confirm this behavior. Although long, closely spaced gill rakers typical of suspension feeders are absent in this species, scanning electron microscopy showed denticles on the branchial surfaces which could trap particles.

Schmitt (1982) observed cooperative feeding behavior by yellowtail (*S. lalandi*) in two locations. At Santa Catalina Island, CA, seven yellowtail swam parallel to shore along the seaward flank of a school of over 2,000 jack mackerel (*Trachurus symmetricus*). The yellowtail split a small group of prey from the school, herded it shoreward toward a rocky coast, and surrounded

it. When the isolated prey then formed a dense aggregation, one yellowtail rushed through and scattered it toward the surrounding predators.

At Danzante Island, Mexico, in the Gulf of California, Schmitt observed three episodes in which groups of 8 to 15 yellowtail formed a line parallel to the reef and approached schools of 700 to 1,000 Cortez grunts (*Lythrulon flaviguttatum*), then broke into two lines and separated small groups of about 15 grunts from the school. The yellowtail drove the small groups away from the reef, presumably to keep them from taking cover in crevices, then encircled and attacked them. Schmitt points out that in addition to demonstrating cooperative feeding, these episodes show that yellowtail's foraging behavior is plastic enough to respond to different prey species and habitats, and provides convincing evidence that yellowtail forage diurnally since these encounters took place in mid-day.

S. rivoliana is described by Myers (1991) as a roving predator of small fishes, but no other information on feeding could be found.

Leatherbacks, or lai (*Scomberoides lysan*) show an interesting ontogenetic shift in diet. Major (1973) observed individuals in Kane'ohē Bay from 27 to 52 mm SL swimming alongside and almost in contact with silversides (*Pranesus insularum*) of 35 to 75 mm SL for several minutes, then striking the silversides along the dorsal surface and sides. In the lab, lai below 150 mm SL demonstrated the same behavior with mullet (*Mugil cephalus*) from 40 to 150 mm SL. The lai were immediately sacrificed and their stomach contents examined, which were found to contain scales and epidermal tissue. Further examination of stomach contents from preserved specimens also resulted in the presence of scales in lai below 150 mm SL.

The diet of lai below 50 mm SL consists of scales and epidermal tissue of schooling fishes. At 50 mm SL the outer dentary teeth of juvenile lai begins to be replaced, and the fish shifts its diet to include whole schooling fishes and crustaceans in addition to scales. By 150 mm SL the lai's dentition is completely replaced by adult teeth, and the fish becomes fully carnivorous. Gerking (1994) notes that scale eaters generally do no particular damage to their host, but Major found that lepidophagous lai often struck the same spot on mullet and silversides repeatedly and caused bleeding.

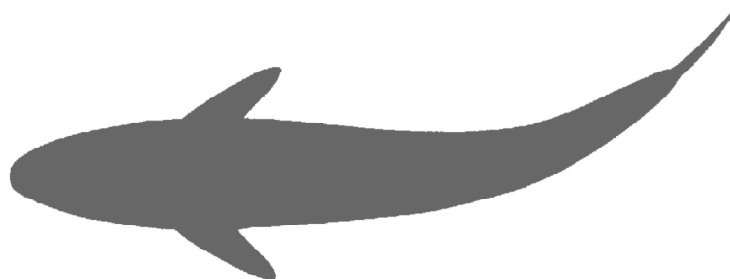


Figure 12

The carangiform mode of swimming. After Bond (1996).

Behavior

Carangids exhibit the carangiform mode of swimming (Figure 12), obviously named for this group of fishes. The anterior one-half to two-thirds of the body bends only slightly while swimming, and most of the thrust is generated in the rear third. The characteristic narrow caudal peduncle and high aspect ratio forked caudal fin serve to increase the efficiency of the tail (Bond 1996). The scutes, when present, probably help reinforce the narrow peduncle (Randall 1983). Because of the caudal fin's stiffness, small changes in direction must be made by other fins.

Holland et al. (1996) studied fine scale movement of 'ōmilu (*Caranx melampygus*) in Kane'ōhe Bay. They found 'ōmilu utilized different parts of the reef at different times, often staying near a particular reef during the day and moving to an adjacent reef at night. Most fish showed strong site fidelity, and didn't move far from the point of release.

Sub-adult akule (*Selar crumenophthalmus*), known as halalū, form large schools in shallow water from about July through December. Eventually they join up with adult schools, which apparently do not make any large scale movements, even around the same island (DLNR 1979). As has been mentioned previously, some carangids form associations with other fishes. Examples include 'ōmilu following blue goatfish, and the relationship between pilotfish and other large carnivores.

Schooling behavior and habitat preferences for Hawaiian carangids are summarized in Table 8.

Species	Schooling; habitat
Scomberoidini	
<i>Scomberoides lysan</i>	Often schools near surface; clear lagoons to offshore reef areas, from surface to 100 m
Naucratiini	
<i>Elagatis bipinnulata</i>	May form large schools; from surface to depths of 150 m or more in clear offshore waters, occasionally in reef areas as shallow as 3 m
<i>Naucrates ductor</i>	Small groups, pelagic, in open waters, commensal relationship with sharks and other large fishes
<i>Seriola dumerili</i>	Solitary or small to moderate schools; reefs or at dropoffs, from 8 to at least 100 m
<i>Seriola lalandi</i>	Large shoals; pelagic and epibenthic, to 50 m
<i>Seriola rivoliana</i>	Outer reef slopes to depths of 160 m or more, perhaps more oceanic than other <i>Seriola</i> spp.
Carangini	
<i>Alectis ciliaris</i>	Adults usually solitary; near bottom in shallow coastal waters to 60 m or more; juveniles pelagic and drifting
<i>Atule mate</i>	Schools; inshore waters to 50 m
<i>Carangoides equula</i>	Benthic, 100 to 200 m
<i>Carangoides ferdau</i>	Coastal waters adjacent to sandy beaches and reefs, to 60 m
<i>Carangoides orthogrammus</i>	Small schools; sandy channels of lagoons, seaward reefs from 3 to 168 m
<i>Caranx ignobilis</i>	Juveniles in small schools over inshore sandy bottoms, adults usually solitary and range widely over reefs to depths of 80 m
<i>Caranx lugubris</i>	Singly or small groups; along outer reef slopes and offshore banks at 12 to 354 m
<i>Caranx melampygus</i>	Singly or small groups; enter channels and inshore reefs to feed
<i>Caranx sexfasciatus</i>	Singly or small groups; in deep channels and outer reefs to 96 m
<i>Decapterus macarellus</i>	Schooling; open water and insular habitats, sometimes at surface, occasionally over outer reefs, usually in waters 40-200 m
<i>Decapterus macrosoma</i>	Schooling; in waters 30-170 m
<i>Decapterus muroadsi</i>	Uncertain
<i>Decapterus tabl</i>	Schooling; midwater or near bottom, in waters 200-360 m
<i>Gnathanodon speciosus</i>	Small schools; adults in seaward reefs, young accompany sharks and other large fish
<i>Pseudocaranx dentex</i>	Schools; banks and inshore slopes in waters 80-200 m
<i>Selar crumenophthalmus</i>	Small to large schools; adults generally offshore in waters to 170 m
<i>Uraspis helvola</i>	Schools; dropoff areas from 30 to 65 m
<i>Uraspis secunda</i>	Small schools; surface, benthic, and pelagic

Table 8

Schooling behavior and habitat for carangids in Hawaiian waters. After Smith-Vaniz (1986b), Smith-Vaniz et al. (1990), Myers (1991).

Predation

Berry (1959) notes that young jack crevalles are food for a number of surface-feeding carnivores. Juveniles of varying sizes were found in the stomachs of fishes as indicated in Table 9. The prey items were apparently not identified more specifically than “jack crevalle.”

Nakamura (1972) makes reference to studies which identified unspecified carangids in the stomach contents of black marlin (*Makaira indica*) in the equatorial Pacific, and *Decapterus* in the same predators off Japan.

In Hawai‘i, halālū (*Selar crumenophthalmus*) ranging in size from four to seven inches are subject to predation by ulua and kawakawa (*Euthynnus affinis*) when they school in shallow water (Gosline and Brock 1960). As mentioned previously, ‘ōpelu (*Decapterus macarellus*) have been found in the stomachs of *Caranx ignobilis* and *Seriola dumerili* in the Northwestern Hawaiian Islands (Sudekum et al. 1991, Humphreys 1986).

Smith-Vaniz and Staiger (1973) describe the venom apparatus of the leatherback (*Scomberoides lysan*). The first seven dorsal fin spines and first two anal spines are associated with venom glands, with the anal spines being the most venomous. The anal spines can be locked outward and inflict painful stings. This is an obvious antipredatory trait, although the identity of the leatherback’s potential predators is not specified.

Hobson (1972, 1974) states that schools of nocturnal carangids, which spend the day hovering in exposed areas near the reef, are targets of larger crepuscular predators, but does not elaborate. Presumably, they may include larger carangids. In general, it’s probable that carangids are potential prey for any piscivore large and fast enough to capture them.

Predator	Max. prey size (mm)
Barracuda, <i>Sphyraena barracuda</i>	167
Greater amberjack, <i>Seriola dumerili</i>	90
Dolphinfish, <i>Coryphaena hippurus</i>	140
Tripletail, <i>Lobotes surinamensis</i>	65
Skipjack tuna, <i>Katsuwonus pelamis</i>	77
Little tunny, <i>Euthynnus alletteratus</i>	28
Blackfin tuna, <i>Thunnus atlanticus</i>	29
Yellowfin tuna, <i>Thunnus albacares</i>	90

Table 9

Predators on carangids, and maximum sizes of jacks found in stomach contents.
After Berry (1959).

Morbidity and Mortality

Thompson and Munro (1974) state that there is “no evidence” regarding factors causing morbidity and mortality in carangids, and their major predators are unknown. The flesh of large kāhala (*Seriola dumerili*) is often infested with larval tapeworms, a condition that occurs in other geographic areas as well. It is uncertain what effects these parasites have on the fish. Kāhala and a number of other carangids are also prone to ciguatoxicity here and in other parts of the world, but the effects of the toxin on the fish is also unknown.

Kawamoto (1973) estimated natural mortality rate of akule (*Selar crumenophthalmus*). The mean monthly survival rate was calculated to be 66.3%, so mortality was 33.7%. Estimated annual survival was then 0.7%, and annual mortality 99.3%. No other data on morbidity or mortality in carangids could be found.

Ecologic Interactions

Since many carangids obtain their food from reef areas, they would be expected to compete with other reef carnivores (Thompson and Munro 1974). Sudekum et al. (1991) estimated average daily consumption rates for *Caranx ignobilis* and *C. melampygus*, then extrapolated to calculate individual food rations for each species per year. Individual *C. ignobilis* were estimated to consume an average of 150.69 kg/yr, and *C. melampygus* an average of 47.82 kg/yr. Based on population estimates at French Frigate Shoals of 130,000 and 230,000, respectively, this resulted in a total consumption of 30,600 tons per year by just these two species.

The estimates, however crude they may be, emphasize the importance of these two species as apex predators both to their own populations and those of their prey. A low overlap of specific diet items indicates they do not compete much with each other. The authors suggest the two species represent one of the most important top-level trophic paths in the French Frigate Shoals ecosystem, and probably many others. Their combined predation pressure exceeds the combined estimate for the three major shark species in the area (gray reef (*Carcharhinus amblyrhynchos*), Galapagos (*C. galapagensis*), and tiger (*Galeocerdo cuvier*), as determined by De Crosta et al. (1984)) by a factor of about 40.

No further information could be found on the ecology of local carangids. All provide food for other fishes at some point in their lives, and the smaller schooling species are probably important food items for larger carnivores, as noted earlier. It is likely that predation by reef-associated carangids upon new recruits, juveniles, and adult prey items plays an important role as described by Hixon (1991) for piscivores in general structuring abundance, distribution, and local diversity in reef fish communities, and reducing intra- and inter-specific competition as a result of postsettlement mortality.

Economic Importance

Carangids have received attention in various parts of the world during the past 30 years or so as potential aquaculture candidates. Most work in the United States has focused on the Florida pompano (*Trachinotus carolinus*), permit (*Trachinotus falcatus*), and palometa (*Trachinotus goodei*). The white trevally (*Pseudocaranx dentex*) is extensively cultured in net cages in Japan, and 1990 production was 959 metric tons (Ogawa 1992). In this species, parasitic and viral infections present problems that must be overcome (Ogawa 1992, Nguyen et al. 1996). Marino et al. (1995) note that the greater amberjack (*Seriola dumerili*) has considerable aquaculture potential due to its rapid growth rate and commercial value, but neither sexual maturity nor gamete release has yet been achieved in captivity.

In Hawai‘i, spawning of akule (*Selar crumenophthalmus*) has been accomplished in captivity, but larval survival to day 75 was less than 3% (Iwai et al. 1996). The Oceanic Institute on O‘ahu has recently developed techniques for culture of ‘ōmilu (*Caranx melampygus*) (Ostrowski pers. comm.).

As indicated earlier, state law prohibits the taking of ulua and papio under seven inches in length for personal consumption. Sale of ulua and pāpio is prohibited for fishes under a pound. There is, therefore, no aquarium fishery for carangids in Hawai‘i, and the small specimens seen in some local pet stores are imported.

A number of carangids have important commercial fisheries in Hawai‘i. Akule are generally taken by handline and surround net. The efficiency of the latter method increased considerably after World War II with the introduction of spotter aircraft, a technique still in use. ‘Ōpelu (*Decapterus macarellus*) are considered an excellent food fish, and are taken by handline and hoop nets (Shiota 1986a).

Commercial fishing for ulua aukea (*Caranx ignobilis*), ‘ōmilu, and *Pseudocaranx dentex* is done mostly by handlines and traps. Commercial catches of carangids for 1998 as reported to the Division of Aquatic Resources are summarized in Table 10.

The palatability of carangids in general ranges from excellent to poor, and some species caught by recreational fishers are not eaten (McClane 1974, Porter pers. comm.). Most local species are considered good eating, although ciguatera poisoning is a concern, especially among the larger reef-associated species. Kāhala (*Seriola dumerili*) are excellent fighters, but are invariably released due to their reputation as a species particularly prone to ciguatoxin. The following information on recreational fishing comes from Rizzuto (1977, 1983), Sakamoto (1985, 1988), and personal observations.

Species	Pounds Landed	Pounds Sold	Value (\$)
Akule and halālū, <i>Selar crumenophthalmus</i>	1,311,201	1,177,018	1,619,594
‘Ōpelu, <i>Decapterus macarellus</i>	234,376	221,678	375,971
Ulua/pāpio (misc.)	39,770	31,020	62,010
“Buta” ulua, <i>Pseudocaranx dentex</i>	40,522	37,953	53,643
Ulua aukea, <i>Caranx ignobilis</i>	9,280	8,614	12,291
Ulua “papa,” <i>Carangoides orthogrammus</i>	3,878	3,438	6,923
“Dobe” ulua, <i>Uraspis helvola</i>	4,118	4,118	6,903
Kamanu, <i>Elagatis bipinnulata</i>	3,394	2,727	3,836
Ulua kihikihi, <i>Alectis ciliaris</i>	2,052	1,191	2,343
‘Ōmilu, <i>Caranx melampygus</i>	1,737	1,125	2,139
‘Ōmaka, <i>Atule mate</i>	237	220	743
Pake ulua, <i>Caranx sexfasciatus</i>	297	278	345
‘Ōpelu “mama,” <i>Decapterus muroadsi</i>	32	26	51

Table 10

Commercial catches and sale of carangids from Hawaiian waters, calendar year 1998, sorted by value. From Division of Aquatic Resources (1998).


Kāhala and kamanu (*Elagatis bipinnulata*) are often caught with shorecasting gear, especially in areas where the bottom drops off rapidly into deep water. They are occasionally caught by trolling, but mostly by bottom fishing from boats.

Lai (*Scomberoides lysan*) are popular sportfish on ultralight tackle, whipping lures or baits just below the surface. They are not highly prized as food fish, but their tough skin (hence the name “leatherback”) is often stripped off, dried, and used for trolling lures.

As mentioned previously, young akule, or halālū, frequently form large schools close to shore from July through December, often entering bays and harbors. During the peak months of July and August recreational anglers are out in force with fiberglass or bamboo handpoles. Adult akule are caught handlining from boats at night, using lights to attract plankton and eventually the fish. ‘Ōpelu are usually taken by sportfishers jigging from boats. Both akule and ‘ōpelu are good eating, but are also used as bait, either cut or whole, for larger fishes.

Ulua and pāpio are highly sought after by recreational fishermen, and ulua are considered by many to be the ultimate shoreline sportfish. Ulua are caught with slide-bait from rocky cliffs, by whipping plugs and bait from boats or shore, and by bottom fishing from boats. They are also taken by spearing, as was the case with the Hawai‘i record 191-pounder. Pāpio are taken

with lighter tackle, mostly by whipping plugs, soft plastics, and bait, but also by dunking bait, trolling, and spearing.

In part because Hawai‘i does not require a marine recreational fishing license, there is no direct data on the economic value of carangids in the state’s recreational fishery. Most sportfishers target them at one time or another. The casting gear required for ulua fishing is expensive, and considering the number of ulua fishermen seen on shorelines around the state, their contribution to the local economy is significant. Gaffney (pers. comm.) estimates the value of the recreational ulua fishery on Hawai‘i’s economy at over \$31 million annually, far exceeding the economic impact contributed by commercial fishing of carangids. 

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